THE UNUSUAL BRACHIAL SKELETON OF *ATTENUATELLA CONVEXA* SP. NOV. (BRACHIOPODA)

by JOHN ARMSTRONG

ABSTRACT. Excellently preserved specimens of *Attenuatella convexa* sp. nov. have enabled reconstruction of a unique brachial skeleton for *Attenuatella*. Apart from this characteristic the genus is closest to members of the Ambocoeliinae (Spiriferida) and its inclusion in this subfamily is still the most plausible supra-generic grouping. Globally, eleven species of *Attenuatella* are now documented and the known range of the genus is from the lower Artinskian (Aktastinian) to the Kazanian or Wordian Stage. The species *Attenuatella convexa* sp. nov., *Attenuatella* sp. A, and *Attenuatella* sp. cf. *incurvata* Waterhouse are here described from Queensland.

ATTENUATELLA STEHLI (1954) is a small, very distinctive spiriferid which occurs at only a few localities throughout the world. The genus has recently been documented from Australia by Waterhouse (1967) and by Armstrong and Brown (1968) who describe species from New South Wales and Queensland respectively. Several additional occurrences are known from the Permian faunas of Queensland and the species from these are described here. Serial acetate peels of well-preserved specimens of one of these species, *Attenuatella convexa* sp. nov., have supplemented the hitherto only fragmentary information that is available about the brachial skeleton of the genus.

Specimens of *Attenuatella* from a number of the localities in Queensland were kindly lent by Dr. J. M. Dickins of the Bureau of Mineral Resources, by Dr. J. F. Dear of the Geological Survey of Queensland, and by Dr. B. N. Runnegar of the University of Queensland. Dr. Dickins made available specimens which he collected from three localities in the Bowen Basin, and Dr. Dear and Dr. Runnegar each supplied a specimen which they had collected from the Barfield Formation in the Bowen Basin, and from just below the Upper Limestone near Gympie respectively. Bureau of Mineral Resources localities referred to, occur on the Duaringa and Taroom 1:250,000 military maps and are designated by a number prefixed by Du and T respectively. Geological Survey of Queensland, and University of Queensland Department of Geology and Mineralogy locality numbers are prefixed by GSQL and UQL respectively. All specimens mentioned have individual numbers which follow the initials of the institution in which the specimens are housed; CPC, Commonwealth palaeontological type collection, Bureau of Mineral Resources, Canberra; GSQF, Geological Survey of Queensland; UQF, Department of Geology and Mineralogy, University of Queensland.

Order SPIRIFERIDA Waagen 1883
Subfamily AMBOCOELIINAE George 1931

Remarks. The brachidia of *Attenuatella* are unusual and are very distinctive. Serial acetate peels prepared from ten specimens of *Attenuatella convexa* sp. nov. do not show any traces of spiralia but they reveal the structures shown in text-fig. 1. Waterhouse (1964) has also figured serial sections of specimens of a species of *Attenuatella*. He found that each brachidium in specimens of *A. incurvata* Waterhouse consisted of an anteriorly directed lamella which at the front of the shell gives rise to a semicircle-like structure parallel to the hinge of the shell (Waterhouse 1964, fig. 48). The brachidia of the

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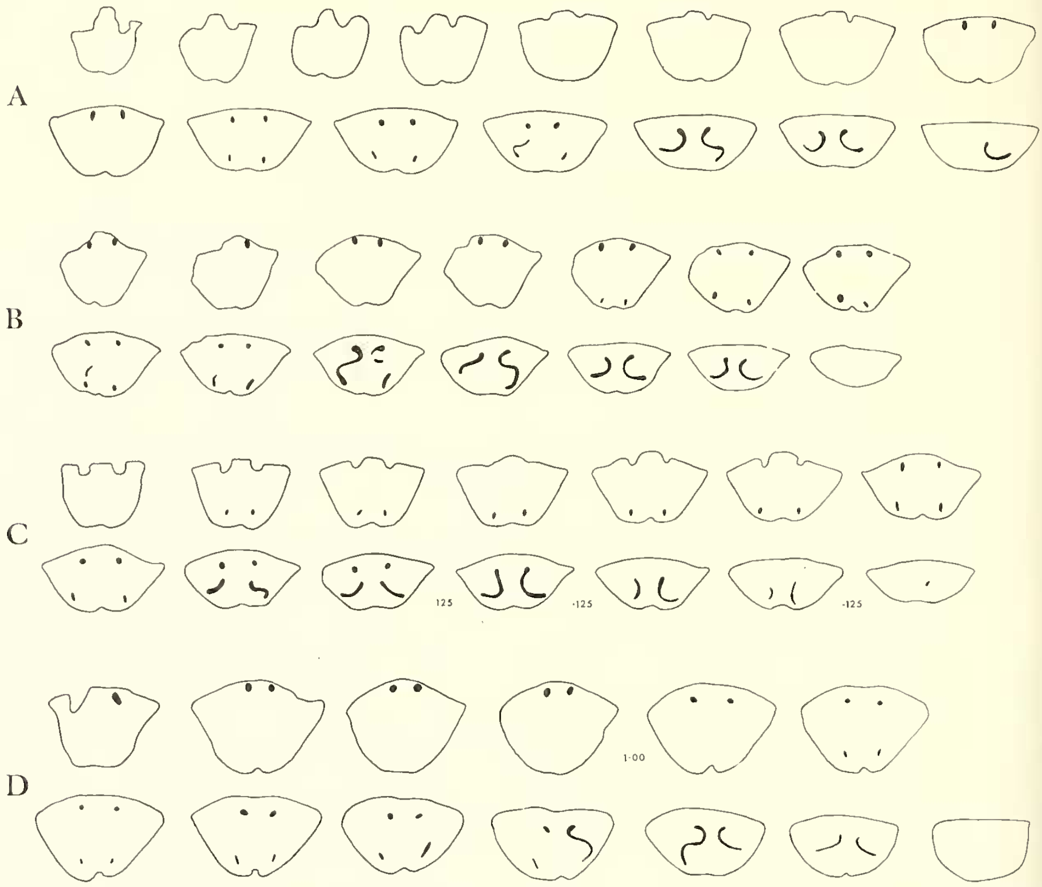
sectioned specimens of *A. convexa*, although initially similar to the preserved brachidia of *A. incurvata*, are more complete and they have enabled reconstruction of brachidia presumably characteristic of the genus (text-fig. 2) though those of the type species are unknown. Each brachidium of *A. convexa* consists of an anteriorly directed lamella

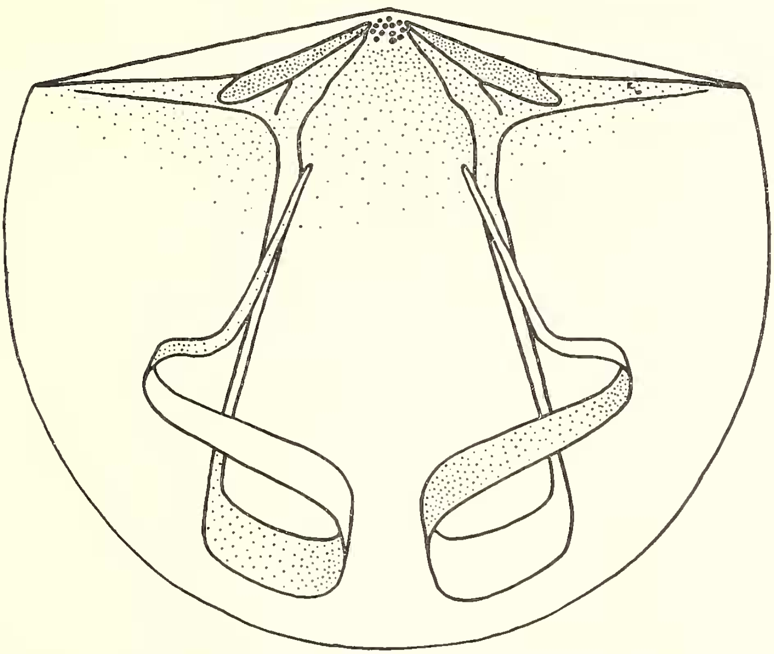


TEXT-FIG. 1. Serial acetate peels of four (A, B, C, D) specimens of *Attenuatella convexa* sp. nov. The interval between successive sections is 0·25 mm. except where indicated, and in the latter cases the dimensions given on the diagram are in millimetres.

which leads into an S-shaped structure (text-fig. 1) from the ventral end of which there is a ventrally placed posteriorly directed lamella. The consistency of the arrangement of these features in the sectioned specimens of *A. convexa* suggests that they represent the complete brachial skeleton of the species. Spiral lamellae are not present in *A. convexa* but rather the brachial skeleton is basically loop-like with curious anterior modifications.

The nature of the brachidia of *Attenuatella* does not necessitate its reclassification. Indeed except for the fact that the spiralia characteristic of several members of the Ambocoeliinae (George 1931, Veevers 1959, Vandercammen 1956) are absent from

Attenuatella, the characteristics of *Attenuatella* completely support its classification in this subfamily. *Attenuatella* has an impunctate shell, a shell form which is comparable with other ambocoelins, a spinose micro-ornament, areas on both valves, and a non-striated tuberculate cardinal process. The placement of *Attenuatella* in the Ambocoeliinae is therefore maintained. A spiriferid having abbreviated brachidia resembling those of *Attenuatella* is the Middle Ordovician genus *Protozyga*. *Protozyga* possesses a jugum but otherwise each of its brachidia has the same basic form of a single volution parallel to the median plane of the shell as the brachidia of *Attenuatella*.



TEXT-FIG. 2. Diagrammatic reconstruction of an antero-ventral view of the brachidia of *Attenuatella convexa* sp. nov., based on serial acetate peels of ten specimens, four of which are shown in text-fig. 1.

The reason for the brachidial deviation in *Attenuatella* from the normal type of spiriferid spiral is problematic and it is conjectural whether the lophophore of *Attenuatella* had the form of a spiral. The shape of the brachidia of *A. convexa* does not preclude the presence of a spiral-like lophophore, and if such an organ did exist it appears that in general only the first flexured whorl of the lophophore was provided with a calcareous support. If the lophophore was not spirolophous but rather was confined to the reduced brachidia it is possible that the S-shaped brachidial modifications were developed to compensate the loss of length of the lophophore. In this instance the feeding organ was probably zygolophous. The brachial skeleton of *Attenuatella* seems to be of a more primitive type than the spiralia of other ambocoelins. Perhaps it is relevant that species of *Attenuatella* are the youngest known representatives of the Ambocoeliinae and that reversion to this loop-like arrangement in *Attenuatella* occurred not long before the extinction of the subfamily in the Upper Permian.

Genus ATTENUATELLA Stehli 1954

Attenuatella Stehli; Chernyak 1963
Attenuatella Stehli; Waterhouse 1964

Type species (original designation). *Attenuatella texana* Stehli 1954, pl. 25, figs. 31–3 from the lower part of the Lower Permian Bone Spring Formation, Texas, text-fig. 3 (1).

Diagnosis. Small essentially plano-convex spiriferids; ventral valve elongate, smooth, or sulcate, with elongate relatively narrow umbo and more or less incurved beak; ventral area apsacline; dorsal valve convex, flat, or gently concave with low area; ornament of small spines often arranged in concentric lines, and fine discontinuous radial grooves; each groove runs anteriorly for a short distance from a spine; field of muscular attachment in ventral valve an elevated platform; no plates support the teeth; crural plates sessile and cardinal process tuberculate; shell impunctate.

Other species and specimens

A. acutirostrus (Krotova) 1885, pl. 4, fig. 24 of Artinskian age from the Ural Mountains in Russia, text-fig. 3 (2).

A. stringocephaloides (Chernysheva and Likharev) *in* Likharev and Einor 1939, pl. 13, fig. 5*a*, *b* from Abrosimov Bay, Novaya Zemlya, text-fig. 3 (3). According to Likharev and Einor (1939, p. 189) a number of the species occurring with *A. stringocephaloides* at Abrosimov Bay (Likharev and Einor 1939, p. 185) also occur in the Spirifer Limestone and Brachiopod Chert in Spitzbergen. Likharev and Einor further intimate (p. 188) that all of the faunas of Novaya Zemlya are to be equated with the faunas of the Spirifer Limestone and the Brachiopod Chert for which Stepanov (1957) has suggested either an upper Lower Permian or a lower Upper Permian age or perhaps both (i.e. belonging to his Svalbardian Stage).

A. attenuata (Cloud) 1944, pl. 17, figs. 22–5 from the Wordian *Waagenoceras* Zone in Mexico, text-fig. 3 (4).

A. stringocephaloides (Chernysheva and Likharev); Chernyak 1963, pl. 42, figs. 3 and 4 from the lower Baykura sub-horizon of eastern Taimyr, text-fig. 3 (5). Ustritskiy and Chernyak (1963) correlate the lower Baykura sub-horizon with the lower Vorkuta Series in the Pechora Basin and they consider that both of these units correspond to the Ufa Suite on the Russian Platform. Stepanov (1957) intimated that the latter Suite should be included in the Svalbardian Stage which he proposed (1957) for faunas in Spitzbergen intermediate in aspect between the faunas of the Artinskian Stage and the Kazanian Stage. For this time interval Ustritskiy (1960) also proposed a new stage, the Paykhoyian Stage based on the fauna of the Vorkuta Series, and in 1963 Ustritskiy and Chernyak had little hesitation in referring the fauna of the lower Baykura sub-horizon to the upper part of Ustritskiy's stage. Ustritskiy and Chernyak also suggest, in view of the absence of a complete Permian section in Spitzbergen, that it might be preferable to recognize the Paykhoyian Stage rather than the Svalbardian Stage.

A. taimyrica Chernyak 1963, pl. 42, figs. 5–9 from the Byrranga horizon of eastern Taimyr, text-fig. 3 (6). Ustritskiy and Chernyak (1963) correlate the Byrranga horizon with a composite Artinskian–Kungurian Stage in the Ural Mountains.

A. incurvata Waterhouse 1964, pl. 20, figs. 1–12, pl. 21, figs. 1–9 from the Arthurton Group in New Zealand, text-fig. 3 (7). Waterhouse (1964, 1967) considers the fauna in this unit to be of Kazanian age.

A. sp. Landis and Waterhouse, 1966, pl. 1, figs. 1–5 from the Wesney Siltstone in the Eglinton Volcanics, New Zealand, text-fig. 3 (8). Landis and Waterhouse seem to be uncertain about the age of these specimens. They firstly state (p. 139) that the specimens 'are probably identical with Aktastinian (lower Artinskian) *Attenuatella* in the Takitimu Group', but later (p. 145) intimate a Kazanian age from their remark regarding the age of the Wesney Siltstone, that 'a Kazanian age is possible on an objective consideration of the fossils alone'.

A. sp. Landis and Waterhouse 1966, p. 144 also mention some specimens of *Attenuatella* from New Caledonia, and after a preliminary examination of the material they consider that the specimens could be conspecific with *A. incurvata*, text-fig. 3 (9).

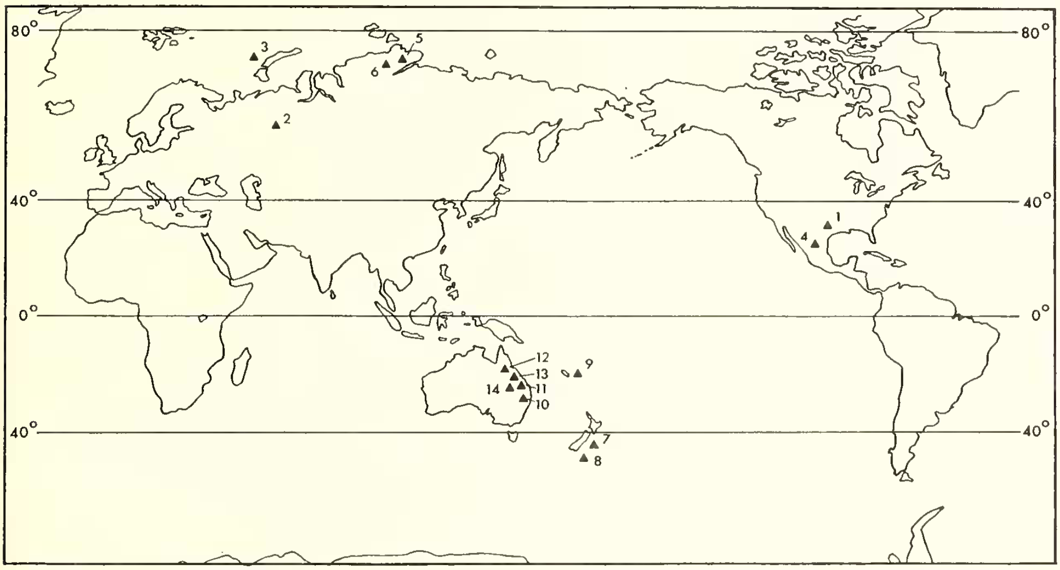
A. multispinosa Waterhouse 1967, pl. 24, figs. 1–7 from the Gilgurry Mudstone in the Boorook Group in northern New South Wales, text-fig. 3 (10). Waterhouse (1967, p. 172) considers that this species is likely to be of late Kungurian or early Kazanian age.

Australis Armstrong and Brown (1968) describe a new species from below the Gigoomgan Limestone in the Maryborough Basin, Queensland, text-fig. 3 (11). They suggest a lower Artinskian (Aktastinian) age for the species.

A. convexa sp. nov. (see p. 788), text-fig. 3 (12).

A. sp. A (see p. 790), text-fig. 3 (13).

A. cf. *incurvata* (see p. 791), text-fig. 3 (14).



TEXT-FIG. 3. Global distribution of *Attenuatella*. Each solid triangle signifies at least one occurrence of the species nominated by the adjacent number. References to the numbers are in the text.

Comparison. Attenuatella is distinguished from *Crurithyris*, its closest relative by its narrower more elongate ventral valve and umbo, and the elevated platform of muscular attachment in the ventral valve. It is also possible to separate the genera on the nature of their brachidia. The brachial skeleton of *A. texana* is unknown. However, from the work of Waterhouse (1964) and from information gained from *A. convexa* it is known that each brachidium of these two species of *Attenuatella* consists essentially of an anteriorly directed lamella which eventually curves ventrally and then is deflected posteriorly to form a single volution parallel to the median plane of the shell. In contrast the brachial skeleton of *Crurithyris urii* (Fleming), the type species of *Crurithyris*, consists of laterally directed spires of from three to six whorls (George 1931, p. 40). Waterhouse (1964, p. 108) has further noted that on *I. incurvata* only one series of spines seems to be present whereas according to George (1931, pp. 51 and 55) there are two series of spines on *C. urii*. However, these differences may not be significant for on some specimens of *A. convexa* the spines are relatively uniform in size, and on others there are both large and small spines (Pl. 142, figs. 5, 12).

Another genus superficially similar to *Attenuatella* is *Mounina* Fredericks 1919

(1924), but unfortunately this genus has been little used or described since its institution. Moreover, the only description of *M. incertia* (Chernysheva), the type species of *Moumina* (OD; Fredericks 1919) is Chernysheva's original description of the general external appearance of the species.

Distribution. In addition to its occurrence in Australia, *Attenuatella* is found in New Caledonia, Russia, North America, and New Zealand. The global distribution is shown in text-fig. 3.

Range. Lower Artinskian (Aktastinian) to Kazanian or Wordian.

Attenuatella convexa sp. nov.

Plate 142, figs. 1–12, 19

Holotype. UQF53036 from UQL3127 in the lower part of the Tiverton Formation in the north-eastern part of the Bowen Basin, Queensland. (UQL3127, about half a mile east of Homevale Homestead, 20 miles north of Nebo on the Nebo–Collinsville road.)

Diagnosis. Ventral valve moderately inflated with a distinct sulcus, and a broad massive umbo that is not incurved over the area; commissure ligate; dorsal valve gently

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EXPLANATION OF PLATE 142

All figures are ×4 except where indicated

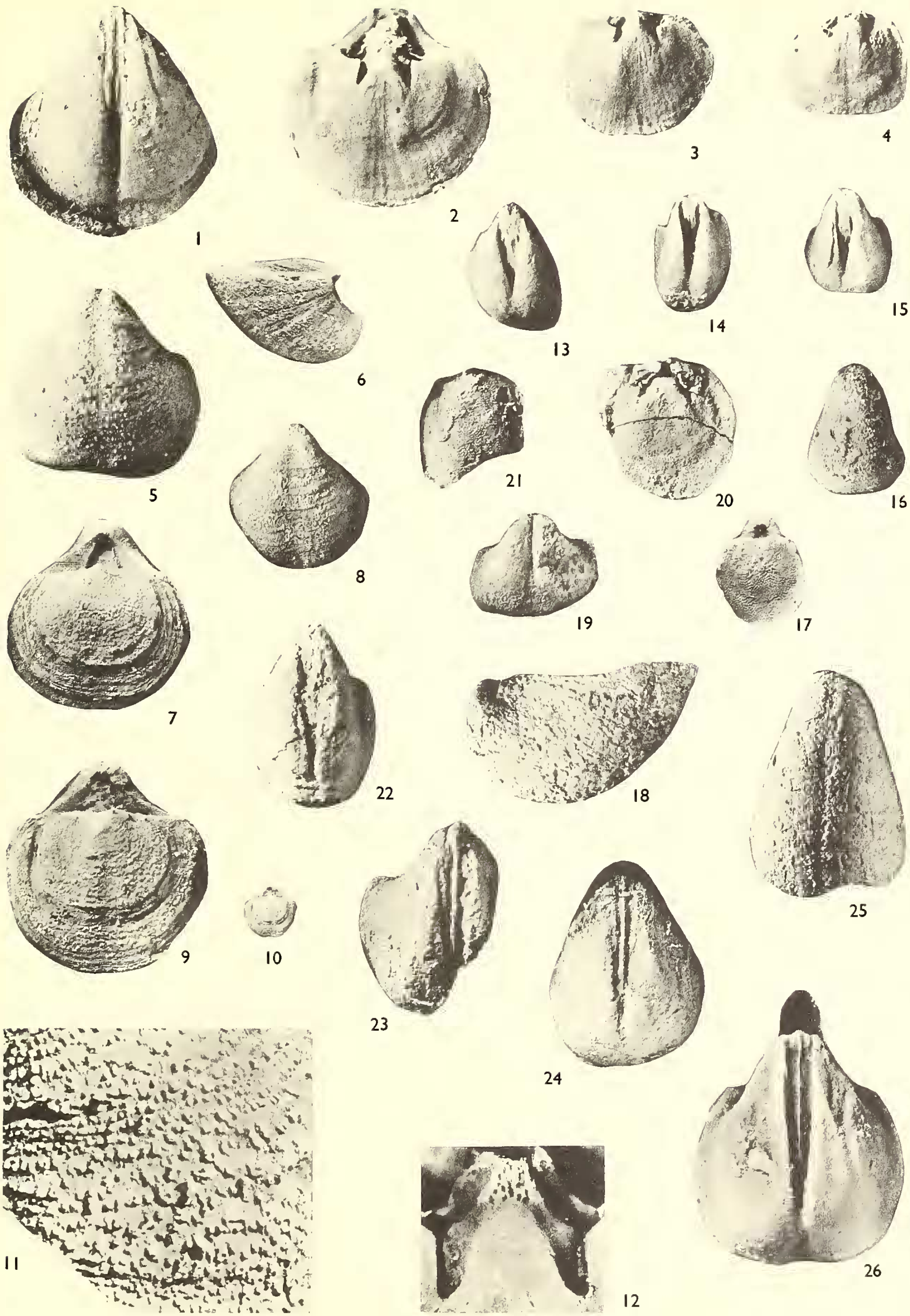
Figs. 1–12. *Attenuatella convexa* sp. nov. All specimens are from the Tiverton Formation at UQL3127, about half a mile east of Homevale Homestead, 20 miles north of Nebo on the Nebo–Collinsville road, Queensland. 1, Internal mould of ventral valve, UQF53029. 2, 3, 4, Internal moulds of dorsal valves (note impressions of areas of adductor muscle attachment in figs. 3 and 4), UQF53030, UQF53031, and UQF53032 respectively. 5, 8, Latex casts from external moulds of ventral valves (note two sizes of micro-ornamental spines on specimen in fig. 5), UQF53033 and UQF53034 respectively. 6, Lateral view of latex cast of external mould of both valves, UQF53035. 7, 9, Latex casts of external moulds of dorsal valve and umbo of ventral valve, UQF53036 (holotype) and UQF53037 respectively. 10, Same specimen as in fig. 9, Natural size. 11, Micro-ornament on a ventral valve ×17 (note the relative uniformity in the size of the spines), UQF53038. 12, Internal mould of the umbonal part of a dorsal valve showing the impression of a tuberculate cardinal process ×12, UQF53039.

Fig. 19. *Attenuatella* sp. cf. *convexa.* Postero-ventral view of internal mould of ventral valve. UQF47256, from the sandstone unit below the Upper Limestone near Gympie. The specimen is from the first ridge north of Rammut Road, three-quarters of a mile east of Chatsworth, 5 miles north of Gympie, south Queensland.

Figs. 13–18. *Attenuatella* sp. cf. *incurvata.* Waterhouse. 13, 14, 15, Internal moulds of ventral valves. CPC9018, CPC9019, and CPC9020 respectively from T111, 2·7 miles north-north-west of the Cracow–Theodore road crossing of Delusion Creek, 10 miles north-west of Cracow, Queensland. 16, Latex cast from an external mould of a ventral valve. CPC9021 from T111. 17, Latex cast from an external mould of a dorsal valve and the umbo of the ventral valve. CPC9022 from T111. 18, Lateral aspect of a ventral valve. CPC9023 from T111.

Figs. 20–3. *Attenuatella* sp. A. 20, Latex cast from external mould of dorsal valve. CPC9027 from T111. 21, Internal mould of dorsal valve. CPC9026 from Du151, 1 mile south-west of Bundaleer Homestead, 37·5 miles north of Bluff, Queensland. 22, 23, Internal moulds of ventral valves. CPC9024 and CPC9025 respectively from Du151.

Figs. 24–6. *Attenuatella* sp. 24, Internal mould of ventral valve. CPC9028 from Du764, 2 miles west-north-west of Bundaleer Homestead 37·5 miles north of Bluff, Queensland. 25, Latex cast of external mould of specimen in fig. 24. 26, Internal mould of ventral valve (note the absence of ridges along the margins of the platform of muscular attachment). GSQF3459 from GSQL D16, in the north-eastern corner of portion 359, Parish Walloon, Queensland.



ARMSTRONG, *Attenuatella*

to moderately convex having a wide median flattening bordered by low ridges for its entire length.

Description. The shell is biconvex with an elongate, moderately inflated ventral valve and a semicircular, gently to moderately convex dorsal valve. Cardinal extremities are obtusely rounded and the shell is usually widest at the mid-length of the dorsal valve. The ventral umbo is high, and relatively broad, but is not incurved over the area. The ventral area is apsacline and is about three times as high as the anacline dorsal area, both areas being separated from the remainder of their valves by distinct beak ridges. There is usually a narrow sulcus in the ventral valve corresponding to a median flattening or depression on the dorsal valve. Flanking the depression on the dorsal valve there are two low ridges. Otherwise the dorsal valve is gently convex, being slightly more so umbonally than towards the commissure. The commissure is ligate. The valves are externally ornamented with small variably sized spines which lie along vaguely concentric lines and are sometimes developed at the edges of growth lamellae. The lines of spines are between 0·1 and 0·3 mm. apart and along them 9 to 12 spines occur in each millimetre. On some specimens there are large spines interspersed with smaller ones (Pl. 142, fig. 5) whereas on other specimens the spines are relatively uniformly sized (Pl. 142, fig. 12). A small groove extends anteriorly for a short distance from each spine.

The internal features of the ventral valve of *A. convexa* are similar to those of *Attenuatella* sp. nov. of Armstrong and Brown (1968). There is little umbonal cavity thickening, and in the apical part of the delthyrial cavity there is a small delthyrial plate somewhat depressed below the level of the area. The musculature is similar to that of *Attenuatella* sp. nov. of Armstrong and Brown except that in *A. convexa* the ridges bordering the muscle platform are less prominent, especially posteriorly; the diductor scars are wider; and the platform of muscle attachment is generally less elevated posteriorly.

In the dorsal valve the sockets are prominent and they lie along the margins of the notothyrium. They are defined internally by prominent socket ridges, and medio-anteriorly confluent with each ridge and extending anteriorly for a short distance along the floor of the valve are the crural bases. From these arise anteriorly directed crural lamellae which give rise to the brachidia diagrammatically represented in text-fig. 2. The arrangement of the scars of adductor muscle attachment is shown in text-fig. 4. The cardinal process occupies the apical part of the delthyrium and is tuberculate, the tubercles being roughly arranged in rows radiating from the beak (Pl. 142, fig. 13).

Comparison. *A. convexa* is readily distinguished by its massive and only gently curved ventral umbo, its broad shell, and its convex dorsal valve. *A. taimyrica* from Russia is the species morphologically closest to *A. convexa*. According to Chernyak's description and figures, *A. taimyrica* shares with *A. convexa* a massive umbo, a gently concave ventral area and a narrow but distinct sulcus. *A. taimyrica* is, however, distinguished by its flat dorsal valve.

Distribution. A specimen from the sandstone unit underlying the Upper Limestone near Gympie is a representative of *Attenuatella convexa*. The specimen is an internal mould of a ventral valve which had a broad massive umbo and a relatively low muscle platform. This is the only known occurrence in addition to the type locality.

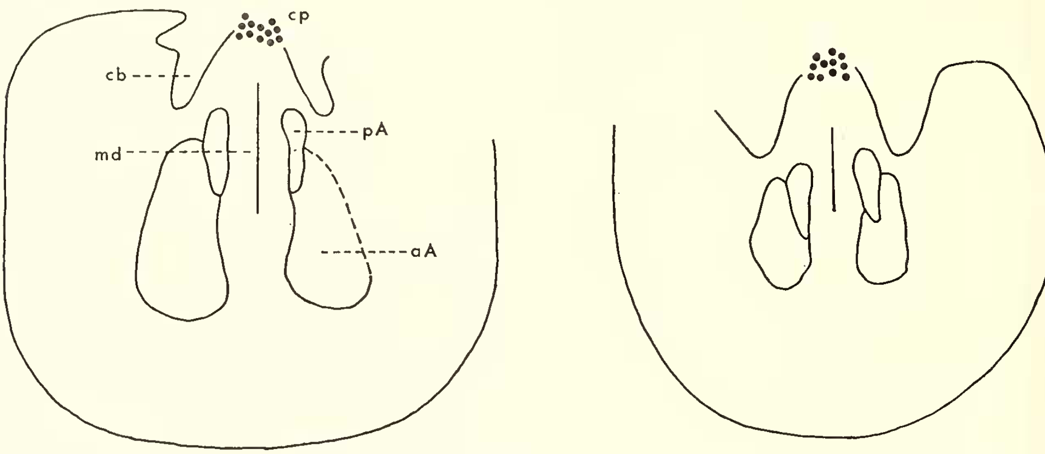
Age. The fauna occurring with *Attenuatella convexa* at the type locality is listed by Armstrong *et al* (1967, p. 89) in their record of the fauna which occurs with *Uraloceras lobulatum* Armstrong, Dear, and

Runnegar. Armstong *et al.* suggest that the most likely age of this fauna is lower Artinskian (Aktastinian) and the similarity between *A. convexa* and *A. taimyrica* provides a measure of support for this determination.

Attenuatella sp. A

Plate 142, figs. 20–3

Material. Several deformed internal moulds of ventral and dorsal valves (CPC9024–6) and a fragment of an external mould from Du151 (1 mile south-west of Bundaleer Homestead 37·5 miles north of Bluff, central Queensland).



A B

TEXT-FIG. 4. Arrangement of the scars of muscular attachment in two dorsal valves of *Attenuatella convexa* sp. nov. A, UQF53031, and B, UQF53032 are figured respectively in Plate 142 figs. 3 and 4. cp, cardinal process; cb, crural base; md, median depressian; pA, posterior abductor scar; aA, anterior abductor scar.

Description. Contour of ventral valve similar to that of *Attenuatella incurvata*; exterior of ventral valve unknown; dorsal valve gently convex and slightly elongate; it is less convex and narrower than dorsal valves of *A. convexa* but is more convex than dorsal valves of *A. incurvata*; on the fragment of external mould the spines number about 10 to 12 per mm. along roughly concentric lines; the interior of the ventral valve is similar to interiors of ventral valves of *A. incurvata* in that the ridges along the edges of the muscle platform are not as prominent as they are in *Attenuatella* sp. nov. of Armstrong and Brown, or in *A. multispinosa* Waterhouse.

Comparison. Attenuatella sp. A is distinguished from *A. incurvata* and *Attenuatella* sp. of Landis and Waterhouse by its elongate gently convex dorsal valve. *Attenuatella convexa* has a broader shell and a lower, more massive ventral umbo. The most closely comparable species are *A. stringocephaloides* and *A. attenuata* both of which have virtually non-sulcate ventral valves and flat or gently convex dorsal valves. The lack of internal details for *A. attenuata* and *A. stringocephaloides* of Chernysheva and Likharev and the lack of ventral exteriors of *Attenuatella* sp. A precludes complete comparison of these species. The interiors of the valves of Chernyak's specimens of *A. stringocephaloides* are known however and again in one of the ventral valves figured by Chernyak